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ABSTRACT

Sampling by spatially replicated counts (point-count) is an increasingly popular method of estimating population size of organisms. Challenges exist when sampling by point-count method, and it is often impractical to sample entire area of interest and impossible to detect every individual present. Ecologists encounter logistical limitations that force them to sample either few large-sample units or many small sample-units, introducing biases to sample counts. We generated a computer environment and simulated sampling scenarios to test the role of number of samples, sample unit area, number of organisms, and distribution of organisms in the estimation of population sizes using *N*-mixture models. Many sample units of small area provided estimates that were consistently closer to true abundance than sample scenarios with few sample units of large area. However, sample scenarios with few sample units of large area provided more precise abundance estimates than abundance estimates derived from sample scenarios with many sample units of small area. It is important to consider accuracy and precision of abundance estimates during the sample design process with study goals and objectives fully recognized, although and with consequence, consideration of accuracy and precision of abundance estimates is often an afterthought that occurs during the data analysis process.

1. Introduction

Estimation of population size by spatially replicated counts (point-count method) has been used for many large-scale animal-monitoring programs (e.g., North American Breeding Bird Survey, North American Amphibian Monitoring Program, and Christmas Bird Count; Royle, 2004). Such studies attempt to estimate abundance by counting organisms within a sample area on repeated visits to obtain an estimation of site-specific abundance (Otis et al., 1978; Williams et al., 2002). Multiple estimated site-specific abundances can be averaged and combined with covariate data to predict abundance across an area of interest (Royle, 2004). Covariate data also provide an understanding of the relation between abundance and habitat use, which is a fundamental interest of many animal-population investigations (Royle, 2004).

A number of complications are associated with estimating population size from point-count data that arise from choices in how to survey a given area. In situations where it is impractical to sample the entire area in which study organisms inhabit, ecologists must decide how to conduct surveys at smaller scales that can provide reliable estimates to the larger area. In such situations, ecologists must make inferences about non-sampled portions of the area of interest from sampled portions of the area (Royle and Nichols, 2003). Furthermore, most survey methods do not detect all individuals present in the survey area. This problem is often minimized by the use of a detection estimator that quantifies the probability that an individual present in the survey area appears in a count statistic (Royle and Nichols, 2003). Lastly, many investigations of animal population size utilizing spatially replicated counts examine rare or elusive species that exhibit low detection probabilities (McDonald, 2004), and thus are characterized by zero-inflated data (Royle, 2004).

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Design of sampling scenarios (i.e., number of sampling units and area of each unit) for point-count population-estimate surveys can influence number of zero-counts encountered while conducting point-counts, and thus influence accuracy and precision of population estimates. Ecologists must carefully select sampling scenarios that will yield an acceptable level of accuracy and precision, while also bearing in mind the challenges faced when sampling organisms in the wild. Often, ideal sampling designs must be altered due to logistical constraints (e.g., monetary or time). Ecologists typically encounter limitations that force them to sample either few large-sample units or many small sample-units. Zeros in catch data are known to cause complications in statistical analysis (e.g., bias in estimate or overdispersion; Welsh et al., 1996), and thus an ecologist might increase sample unit area to reduce the chance of a zero catch. Likewise, more sample units yield greater statistical power (Cohen, 1977; Thompson, 2012). Thus, a trade-off likely exists between the number of zero-counts encountered and statistical power for ecologists devising survey design to measure population size. Does the trade-off between increasing size of the sample unit and decreasing number of sample units influence accuracy and precision of population estimates derived with point-count methodology?

Though the sampling scenario itself could potentially influence accuracy and precision of abundance estimates, density and distribution of animals within the population of interest could also be influential. Density of a population may affect the ability of an ecologist to detect individuals, and has been reported to affect accuracy and precision of population estimates from visual counts (Heggenes et al., 1990; Rodgers et al., 1992; Pink et al., 2007). Detection probability may be low when sampling low-density populations (Rosenberg et al., 1995; Royle, 2004), due to infrequent encounters of scarce individuals (e.g., endangered species). Alternatively, saturation of sampling gear could produce misrepresentative count data in high-density populations. For example, catchability coefficient (i.e., proportion of individuals caught by each unit of effort) has been reported to vary inversely with abundance, and sampling gear was more effective at lower population density in Chinook salmon *Oncorhynchus tshawytscha* (Peterman and Steer, 1981).

Random distribution of individuals within a population is an assumption made when estimating population size by the point-count method (Royle, 2004). Random distribution rarely occurs in nature, and is probably only justified within a homogeneous landscape (Royle, 2004). Distribution of individuals can be influenced by habitat use and availability (Conroy et al., 2008). When a random sampling design is employed, biased estimates of population size are possible if used habitats are not sampled (Pink et al., 2007). Homogenous landscapes rarely occur in nature and therefore habitat heterogeneity likely influences distribution of individuals and likewise influences detection probability. Heterogeneous detection probabilities are known to occur when estimating population size (Royle and Nichols, 2003), and several models for both occupancy and abundance have been developed to account for heterogeneous detection probabilities (Dorazio and Royle, 2003; Royle and Nichols, 2003; Tyre et al., 2003; Royle et al., 2005). Variation of abundance among sample sites induces site-specific heterogeneous detection probabilities, and can be exploited to model population size assuming spatial distribution of individuals across survey sites follow a prior distribution (e.g., Poisson distribution; Royle and Nichols, 2003). A heterogeneous landscape with variable habitat likely induces heterogeneous detection of individuals and possibly influences accuracy and precision of population estimates derived from the point-count method.

The *N*-mixture model has been used to estimate population size from spatially replicated count data (Royle, 2004). The *N*-mixture model allows for spatial variation in detection and abundance to be calculated directly. The *N*-mixture is unbiased in parameter estimation even when similar covariates are used in both the detection and abundance models (Kéry, 2008). The model integrates the binomial likelihood for observed counts over possible values of abundance for each sample point using a prior distribution on abundance (e.g., Poisson, negative binomial, or zero-inflated Poisson; Royle, 2004). The *N*-mixture model is defined as:

$$n_{it} \sim \text{Binomial}(N_i, p)$$

where n_{it} is the number of distinct individuals counted at location i in time t, N_i is the number of individuals available for sampling (i.e., the population size at location i), and p is the detection probability (Royle, 2004). The likelihood for N_i is then integrated over a prior distribution. The Poisson distribution is a commonly used model for the distribution of organisms. The Poisson mixture estimator is defined as:

$$f(N;\lambda) = \frac{e^{-\lambda}\lambda^{N}}{N!},$$

where N is the number of individuals available for sampling, and λ is mean of Poisson distribution such that N values follow a Poisson distribution with mean λ (Royle, 2004).

Our objective was to examine how different sampling scenarios, given interaction with environmental factors (i.e., true abundance of individuals and distribution of individuals), influences the accuracy and precision of population estimates derived from the point-count survey method. Accuracy and precision of abundance estimates are both desired for development of sound management practices. Therefore, the influence of sample design on accuracy and precision of population estimates derived from the point-count method must be understood to improve management decisions.

2. Methods

2.1. Modeling approach

We applied sampling scenarios to a computer modeled environment to evaluate the influence of sampling-unit size and number on accuracy and precision of point-count population estimates. A virtual environment consisting of a 10×10 matrix was created to assess the influence of sampling-unit size and the number of sample units on the accuracy and precision of population estimates derived from the point-count method. In our simulations, the total area sampled remained constant among the sample scenarios evaluated (i.e., a total of 24 cells sampled of the 100 available), but scenarios ranged from few samples of large area to many samples of small area.

In addition to the number and unit size of the samples, we also examined how true abundance (density) and distribution of individuals influenced accuracy and precision of population estimates. Individual treatments of true abundance and distribution of individuals were assessed simultaneously with sampling scenarios. All possible combinations of sample scenario, true abundance, and distribution of individuals were evaluated.

The number of individuals that could occur within any one cell was constrained only by true abundance. In order to vary whether an individual within a cell was sampled during any of the three sampling events, each individual within a cell was assigned a detection probability for each sampling event from a random uniform distribution between 0 and 1. Individuals were viewed as sampled if the assigned detection probability exceeded the assigned cell-specific detection probability, which introduced habitat-based heterogeneity to the virtual environment (probabilities were derived from a study of largemouth bass *Micropterus salmoides* detection in a small [12-ha] impoundment;

Table 1
Sample unit number and size for sampling scenarios used in simulated replicated counts. Sample units denoted by scenario name (e.g., "2,12" = 2 samples from units of 12 cells each).

Scenario	*N* samples	Sample unit area
2,12	2	12 cells
3,8	3	8 cells
4,6	4	6 cells
6,4	6	4 cells
8,3	8	3 cells
12,2	12	2 cells
24,1	24	1 cell

see Kowalewski, 2014 for further details). Cell-specific detection probabilities ranged between $p = 0.01$ and $p = 0.98$.

The modeled environment had specific protocols to define the sampling process and always progressed in the order of: (1) environment populated with organisms based on defined distribution treatment, (2) detection probability applied to cells, (3) sample locations randomly chosen, (4) sample-count data applied to *N*-mixture model. Assumptions of the modeled environment were: (1) sample events were independent among runs, (2) sample sites were closed between sampling events, (3) the sampler was naive of organism distribution, and (4) once assigned to a cell an individual was constrained to that cell (i.e., no immigration or emigration). One-thousand iterations of each sample scenario, true abundance and distribution of individuals combination were run to determine central tendency of sample scenarios and assess accuracy and precision of population estimates derived from the point-count method.

2.2. Sampling scenarios

Seven different sampling scenarios were evaluated (Table 1). Total area sampled remained constant for each sampling scenario by selecting a total of 24 cells from the available 100 cells (approximating one quarter of the available habitat, but allowing each sample unit area and number of sample units combination to be equally divided by 24). Sample units ranged in area from 1 cell to 12 cells and sample units ranged in number from 24 sample units to 2 sample units (Table 1), and were depicted as "number of samples, unit size" (e.g., "24,1" = 24 samples from units of 1 cell each). Sample units were randomly chosen and consisted of adjacent cells (except for 24,1 scenario; sample unit size = 1 cell) joined edge to edge (no diagonal cells). No overlap among sample units was allowed. For each model run, three sampling events (point-count) were conducted using the same spatial layout of sampling scenario to obtain spatially replicated count data for use in a model to estimate point abundance.

2.3. True abundance of individuals

Ten scenarios of true abundance of individuals were analyzed for each sampling scenario. The true abundance of individuals ranged from 100 individuals and increased by 100 individuals to a maximum of 1000 individuals (true abundance 100–1000 individuals). Evaluating a gradient of abundances from low to high provided a greater understanding of the influence of abundance of individuals on accuracy and precision of population estimates derived from the point-count method.

2.4. Distribution of individuals

Individuals were distributed within the virtual environment by two treatments (uniformed and clustered). Individuals distributed by the uniform treatment had an equal probability (e.g., each individual had a probability of 0.01) of occurring within any cell (Fig. 1).

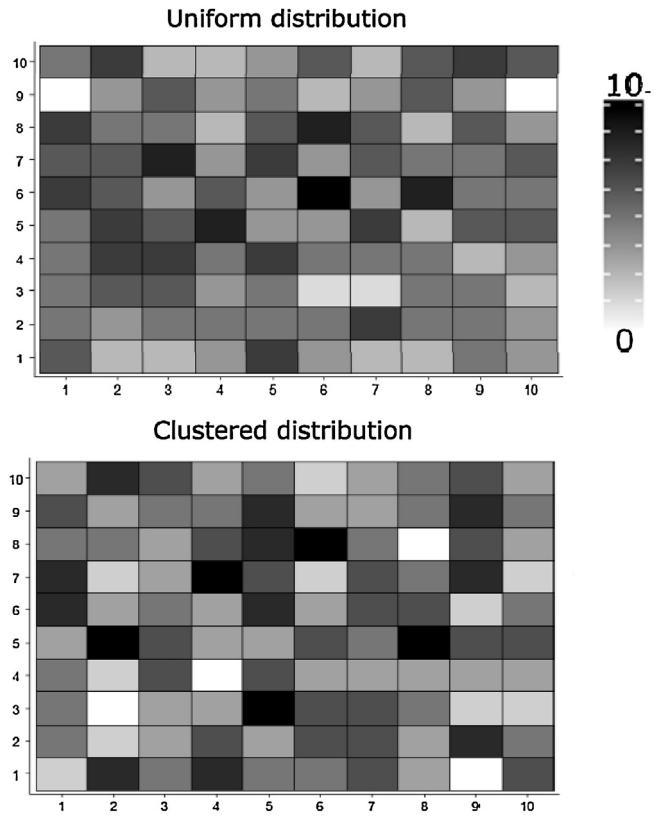

Fig. 1. An example of a uniform and clustered distribution of 500 individuals within the sample space. The number of individuals within a cell range from 0 (white) to 10 (black). In the clustered distribution, the seed cells at are located at 2 (column), 5 (row); 4,7; 5,3; 6,8; and 8,5.

Individuals distributed by the clustered treatment had a greater probability to occur in a cell occupied by another individual. To accomplish this, we randomly selected five seed cells (i.e., centers of the cluster) within the grid that had double the probability occurrence of the uniform probability (i.e., probability = 0.02). Adjacent cells to the seed cells had half the probability of the seed cell (i.e., probability = 0.01). Remaining cells not directly adjacent to seed cells had a lower but equal probability to be occupied (i.e., probability = 0.009). This approach allowed for areas with greater number of individuals surrounded by areas with fewer individuals (i.e., patchy distribution; Fig. 1). There was no limit on the maximum number of individuals that could occur within one cell for both the uniformed and clustered distribution treatments.

2.5. Data analysis

The number of individuals sampled during the three sampling events was used to estimate calculated detection probability and site abundance for all sampled cells using an *N*-mixture model as specified by Royle (2004). The *N*-mixture model allows point detection probability (p) and abundance (λ) to be constant or to vary with specified covariates. The parameters in our model allowed detection probability to vary as a function of visit (i.e., 3 sample events) and abundance to vary by intercept only. The *N*-mixture model provided an estimate of calculated detection probability and abundance for sampled area. Population estimates were derived by area expansion of modeled estimates of detection and abundance from sampled area (Royle, 2004). Estimates were calculated using the "pcount" function in the unmarked package (Fiske and Chandler, 2011) in R (R Development Core Team, 2013). Accuracy of estimates was analyzed by examining median of standardized

differences from true abundance of population estimates across 1000 iterations for each scenario. To calculate standardized difference from true abundance the following formula was applied:

$$\frac{(N_e - N_t)}{N_t}$$

where N_e = extrapolated abundance and N_t = true abundance. Precision of estimates was analyzed by examining median of standardized widths from 95% confidence intervals of population estimates across 1000 iterations for each scenario. To calculate standardized widths from 95% confidence intervals the following formula was applied:

$$\frac{W_e}{N_t}$$

where W_e = extrapolated 95% confidence-interval width and N_t = true abundance. Frequency of population estimates out of 1000 simulations for the seven sampling scenarios in which true abundance was below, within, and above the 95% confidence interval of the population estimate was also calculated to assess accuracy and precision of estimates.

3. Results

A general trend existed for each sample scenario combination in which more sample units of small area had estimates with greater accuracy and few sample units of large area had estimates with greater precision. The 24,1 (24 sample units of 1 cell) sample scenario achieved the most accurate estimates, whereas the 2,12 (2 sample units of 12 cells) sample scenario achieved the most precise estimates (Figs. 2 and 3). Estimates from the 24,1 scenario had large 95% confidence intervals and most frequently the true abundance was within the interval, whereas estimates from the 2,12 scenario had small 95% confidence intervals and most frequently the true abundance was outside the interval (Figs. 2 and 3). As sample scenarios transitioned from many sample units of small area (24,1) to few sample units of large area (2,12), a trade-off between accuracy and precision of estimates existed. Even though estimates from sample scenarios with few sample units of large area had high precision, the estimates tended to underestimate true abundance.

The magnitude of the trade-off between accuracy and precision of estimates was influenced by the true abundance of individuals. The trade-off between accuracy and precision of estimates was greatest for high abundance populations (1000 individuals) and least for low abundance populations (100 individuals). The abundance pattern appeared consistent across all combinations of treatments evaluated.

Similar results were produced for both distribution of individuals treatments (Fig. 2 [uniform distribution]; Fig. 3 [clustered distribution]). The maximum difference between median standardized difference from true abundance of a uniform distribution treatment compared to a clustered distribution treatment from any sampling scenario and density of individuals was 0.03 (mean ± SE = 0.01 ± 0.00; n = 70). The maximum difference between median standardized 95% confidence-interval widths of a uniform distribution treatment compared to a clustered distribution treatment from any sample scenario and density of individuals was 0.42 (mean ± SE = 0.14 ± 0.01; n = 70). Distribution of individuals had minimal influence on the accuracy and precision of estimates generated by modeled sample scenarios, given the similarity of results generated by random and clustered treatments.

4. Discussion

The general trend across the sample scenarios combined with environmental factors we evaluated was that a trade-off exists between accuracy and precision of abundance estimates derived from point-count method. Sample scenarios with many sample units of small area (i.e., 24,1) provided estimates that were consistently closer to true abundance than sample scenarios with few sample units of large area (i.e., 2,12). However, sample scenarios with few sample units of large area (i.e., 2,12) provided more precise abundance estimates with smaller widths of 95% confidence intervals than abundance estimates derived from sample scenarios with many sample units of small area (i.e., 24,1). Although minimal variation of parameters describing accuracy and precision of abundance estimates occurred between true abundance and distribution of individuals, the same general trends remained across sample scenarios. Thus, sample design must be carefully considered as it influences accuracy and precision of abundance estimates. This is important to note because sample design is a factor that is within the ecologist's control, whereas environmental factors are not. It is also important for ecologists to first identify research objectives, and then structure sample design to accomplish those objectives.

Abundance estimates with the greatest accuracy occurred with a greater number of sample units and smaller sample-unit size. More samples may be necessary to provide reasonable estimates of abundance when heterogeneity of count data exists as a result of site abundance (Royle and Nichols, 2003). Sampling larger area reduced variation between count data of sample sites, and thus improved precision of the abundance estimates. Our sampling scheme (number of visits to sample site) was not adjusted to account for heterogeneous detection probabilities. When false-negatives exist (failure to detect an individual when in fact it is present), increased repeated visits eliminated false-negative bias for models of occupancy (Tyre et al., 2003). Further, Tyre et al. (2003) reported that greater efficiency was gained by adding more sample sites when false-negative error rates were $\leq$50%, whereas precision was improved by increasing the number of visits to a sample site, when false-negative error rates were >50%. A greater number of repeated visits could potentially improve accuracy and precision of abundance estimates (Dail and Madsen, 2010).

There have been a number of historical recommendations for estimating sample size requirements. Recommendations include sample size to achieve a desired level of precision (Gunderson, 1993) and sample size based on statistical power (Peterman and Bradford, 1987; Peterman, 1990; Quist et al., 2009). Too few samples may result in an inability to decisively reject hypotheses and this aspect of survey design is often accentuated by low precision frequently associated with sampling gears (Cyr et al., 1992; Hardin and Connor, 1992; Wilde, 1993; Wilde and Fisher, 1996). From our models, if a desired level of precision is the target goal for utility of abundance estimates (e.g., comparison across years) then fewer samples of large area should be a suitable sample design given a finite amount of effort. However, number of samples should be increased if abundance estimates are to be used for hypothesis testing and statistical power is a concern (i.e., the probability of failing to reject a false null hypothesis), because statistical power is a function of sample number. A sample design stratified by habitat type or classes of strata may further increase precision of estimates by reducing sampling variation (Wilde and Fisher, 1996). However, stratification variables must be appropriate surrogate measures to variables of interest (e.g., habitat variables known to be either preferred or avoided by species of interest) for increase in precision of abundance estimates (Wilde and Fisher, 1996).

The true abundance of individuals influenced the magnitude of the trade-off effect observed with accuracy and precision of abundance estimates. Sample design had less of an influence on

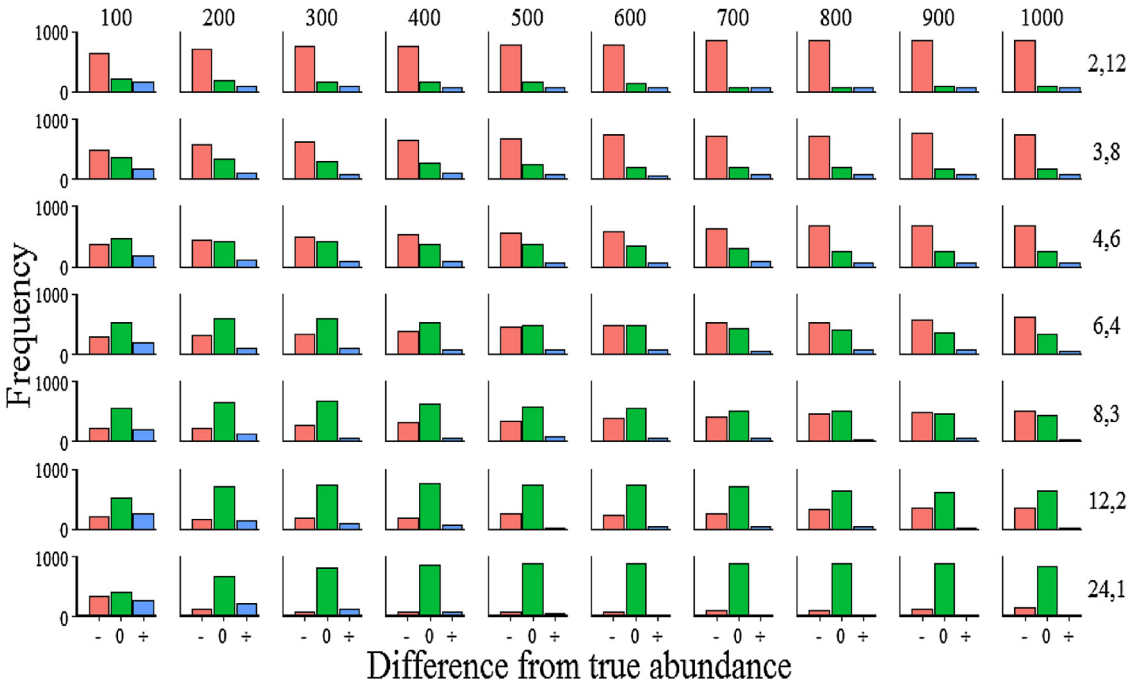

Fig. 2. Frequency of population estimates out of 1000 simulations in which true abundance was below (red), within (green), and above (blue) the 95% confidence interval of the population estimate for 7 sample scenarios (indicated on right of plots) and 10 populations (N = 100–1000, as indicated on top of plots). For modeling, individuals were uniformly distributed across a 10 × 10 grid in which there was no limit on the maximum number of individuals that could occur within one cell.

accuracy and precision of abundance estimates in low abundance populations (100) when compared to high abundance populations (1000). We expected potential accuracy and precision bias at low abundance based on low detection due to infrequent encounters of scarce individuals (Rosenberg et al., 1995; Royle, 2004). Our results were contrary to initial speculation and greater bias occurred at high abundance. We also expected potential accuracy and precision bias due to clustered distribution of individuals based on cell to cell variation. Again our results were contrary to initial speculation and no difference occurred between random and clustered treatments resulting in minimal influence on accuracy and precision of population estimates.

Although our simulations help better understand how sample design influences accuracy and precision of abundance estimates, there are some caveats that should be considered for our model. The size of our virtual environment was designed at a scale that

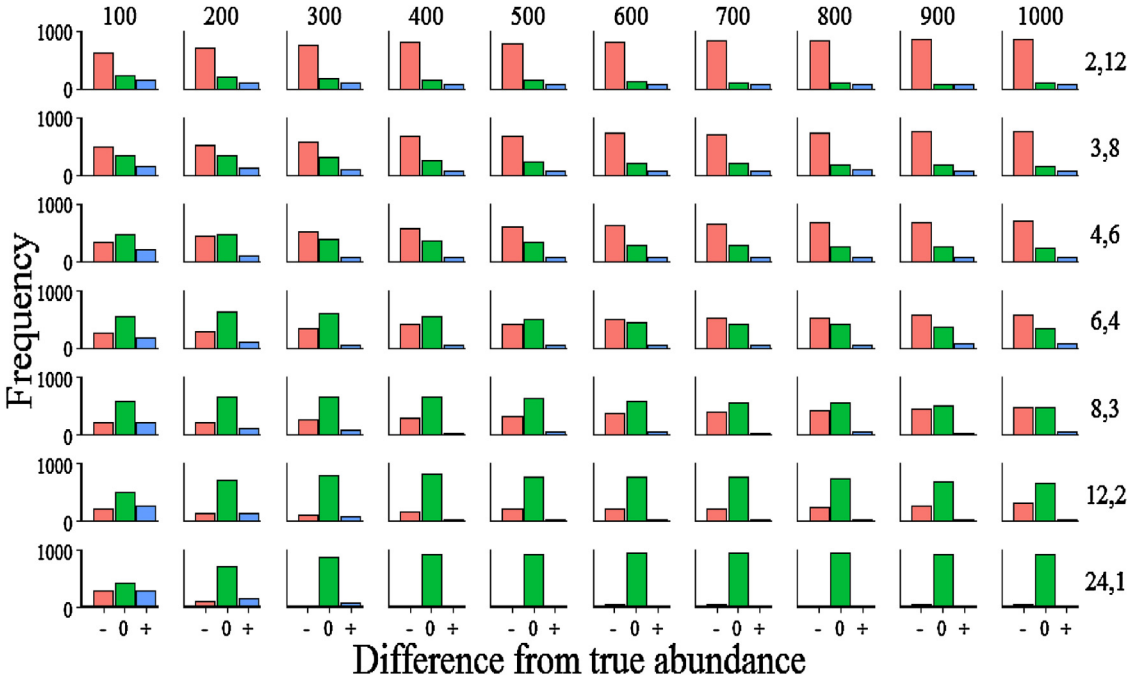

Fig. 3. Frequency of population estimates out of 1000 simulations in which true abundance was below (red), within (green), and above (blue) the 95% confidence interval of the population estimate for 7 sample scenarios (indicated on right of plots) and 10 populations (N = 100–1000, as indicated on top of plots). For modeling, individuals were distributed in clusters across a 10 × 10 grid in which there was no limit on the maximum number of individuals that could occur within one cell.

allowed for examination of plausible sampling scenarios that maintained consistent total area sampled to help guide sampling effort allocation. Sampling scenarios modeled in larger virtual environments containing more grid cells could potentially allow for greater ability to view subtle changes in model results. Our simulations only examined one level of clustered distribution and increasing levels of patchiness should be further evaluated. The number of repeated, sampling events is another important consideration in designing the point-count sampling but was beyond the scope of this study. Further research is needed to examine the influence of adding additional sampling events on accuracy and precision of abundance estimates.

The trade-off between accuracy and precision of abundance estimates is an important aspect for ecologists to consider when devising sampling regimes. It is imperative to consider accuracy and precision of abundance estimates during the sample design process with study goals and objectives fully recognized; unfortunately, and not without consequence, consideration of accuracy and precision of abundance estimates is often an afterthought that occurs during the data analysis process. Precision in abundance estimates is undeniably desired, but from our simulations the sample designs that produced the greatest precision generally underestimated abundance, and would result in biased management decisions. Natural resource managers making management decisions based on abundance estimates would most likely desire an estimate that was both accurate and precise, but in reality, choice of sample design potentially dictates favor towards accuracy or precision in abundance estimates. Is it more valuable to have abundance estimates that are more accurate, more precise, or some optimal combination of both? Consideration of research objectives or management goals must be practiced when selecting sample design for abundance estimates, given that ecologists by default opt for greater accuracy or greater precision by choice of sample design.

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